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Establishment and dominance of an introduced herbivore has limited impact on native host-parasitoid food webs

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Abstract The gypsy moth is considered one of the most harmful invasive forest insects in North America. It has been suggested that gypsy moth may indirectly impact native caterpillar communities via shared parasitoids. However, the impact of gypsy moth on forest insect food webs in general remains unstudied. Here we assess such potential impacts by surveying forest insect food webs in Ontario, Canada. We systematically collected caterpillars using burlap bands at sites with and without histories of gypsy moth outbreak, and then reared these caterpillars until potential parasitoid emergence. This procedure allowed us to generate quantitative food webs describing caterpillar-parasitoid interactions. We estimated the degree of parasitoid sharing between

gypsy moth and native caterpillars. We also statistically modeled the effect of gypsy moth outbreak history and current gypsy moth abundance on standard indices of quantitative food web structure and the diversity of parasitoid communities. Rates of gypsy moth parasitism were very low and gypsy moth shared very few parasitoids with native caterpillars, suggesting limited potential for indirect interactions. We did not detect any significant effects of gypsy moth on either food web structure or parasitoid diversity, and the small amount of parasitoid sharing strongly implies that this lack of significance is not merely due to low statistical power. Our study suggests that gypsy moth has limited impact on native host-parasitoid food webs, at least for species that use burlap bands. Our results emphasize that extrapolations of theoretical and experimental conclusions on the impacts of invasive species should be tested in natural settings.

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Introduction

The establishment of invasive species into native communities can lead to a complex set of consequences. Invasive species add new links to food webs

and can modify the strength of existing interactions (e.g. Pearson and Callaway 2003; Lafferty and Kuris 2009), processes that can facilitate the decoupling of ecological networks, species loss, or even community collapse (McCann 2000; McCann et al. 1998; Dunne et al. 2002; Jonsson et al. 2006; Dunne and Williams 2009). Research on invasive plants (Lopezaraiza-Mikel et al. 2007; Carvalheiro et al. 2008), pollinators (Aizen et al. 2008), and predators (Sanders et al. 2003) has shown that introduced species can alter ecological network structure and affect community organization. However, empirical studies of community impacts of invasive herbivores tend to involve only a few species (e.g. Settle and Wilson 1990; Preisser and Elkinton 2008) and provide little insight on how effects might be scaled up to whole networks of interacting species at multiple trophic levels. Extending our understanding of the impacts of invasive herbivores using food webs will help us to identify the processes and mechanisms involved, providing necessary information for those who wish to predict, prevent, and mitigate those impacts.

The gypsy moth, *Lymantria dispar* (L.), is often described as one of the most serious invasive forest insects in North America (e.g. ISSG 2009), with both economic and ecological consequences for the forests it infests (e.g. Leuschner et al. 1996; Lovett et al. 2006). It has a well-known complex of natural enemies, including over twenty species of native and introduced primary and hyperparasitoids, some of which are also known to attack native forest Lepidoptera (Griffiths 1976; Arnaud 1978; Simons et al. 1979; Nealis et al. 2001; Yu 2009). The gypsy moth feeds on a large variety of native tree species, thus sharing habitat and resources with many native herbivores (Liebhold et al. 1995). The establishment of the gypsy moth therefore adds not only a new herbivore, but also a number of new links into native food webs. Some authors have speculated that the gypsy moth may indirectly affect native species through shared natural enemies (Redman and Scriber 2000; Work and McCullough 2000; Schweitzer 2004; Summerville and Crist 2008). However, while several decades of research have been devoted to the effects of the gypsy moth on trees, forests, and wildlife, no study to date has investigated the impact of the gypsy moth on forest insect host-parasitoid food webs.

In addition to adding new links to native food webs, the presence of the gypsy moth may also affect

the strength of existing interactions. Outbreaks of forest caterpillars can temporarily increase the local abundance and diversity of parasitoids, both by acting as a numerically abundant source of prey (e.g. Eveleigh et al. 2007) and by inducing host plant volatiles that are strongly attractive to parasitoids (e.g. Havill and Raffa 2000). Shared parasitoids can be an important structuring force in insect communities (e.g. Bonsall and Hassell 1997; Van Nouhuys and Hanski 2000; Teder and Tammaru 2003; Van Veen et al. 2006) and can influence the outcome of interactions between invasive and native species (Settle and Wilson 1990; Hoogendoorn and Heimpel 2002; Noonburg and Byers 2005). Gypsy moth outbreaks can cause local population increases in at least some of its natural enemies (Gould et al. 1990), thus creating the potential for parasitoid-mediated indirect interactions between the gypsy moth and native species. Several studies have demonstrated high levels of parasitism in native caterpillars by introduced gypsy moth parasitoids (Schaffner and Griswold 1934; Boettner et al. 2000; Redman and Scriber 2000; Kellogg et al. 2003; Ellis et al. 2005); however, it is unclear whether or not this has been facilitated by the presence of the gypsy moth.

Here we evaluate the impacts of the gypsy moth on native caterpillar-parasitoid communities in northern temperate forests using quantitative food webs. Our study took place on the northern edge of gypsy moth infestation in Ontario, Canada, where outbreaks occurred for the first time in the early 1990s. We chose to work in this region as it was possible to identify sites that had varying histories of gypsy moth outbreak but were similar in regards to other biological and geographical characteristics. Previous work with these data indicated that current gypsy moth abundance was more important than outbreak history in the impact of gypsy moth on native caterpillar communities (Timms 2010). Therefore, we also investigated effects of gypsy moth abundance on native food webs.

Our analytical approach begins by quantitatively estimating the degree of parasitoid sharing between gypsy moth and native caterpillars; parasitoid sharing is a necessary requirement for apparent competition and other parasitoid-mediated indirect interactions, and therefore these estimates establish the degree to which we should expect gypsy moth to have an effect on native food webs. We then ask if gypsy moth had

an effect on food web structure, as measured by quantitative food web metrics. The use of quantitative food webs is a relatively new technique that has successfully been used to address both theoretical and applied ecological issues (Memmott 2009). Quantitative food webs include information on both the presence and magnitude of links between species, allowing predictions about both the potential location and importance of indirect interactions. We also asked if gypsy moth had an effect on parasitoid diversity. We hypothesized that gypsy moth history and abundance should have a detectable effect on food web structure and diversity, provided that gypsy moth shared a wide variety of parasitoid species with native caterpillars; in this way, we assess the impacts of an invasive species on a native food web.

Materials and methods

Sampling and identification

We collected caterpillars from ten northern temperate forest sites over two sample years. Sites were chosen according to their gypsy moth outbreak history, red oak, *Quercus rubra* L., availability, and accessibility by road. The locations of significant defoliation by the gypsy moth in the region were identified with the assistance of the Canadian Forest Service (CFS) Forest Health Survey data, while stand species composition was identified using Forest Resource Inventory maps provided by local forest management companies. Five sites with and five sites without histories of significant gypsy moth defoliation were selected within the Algonquin-Lake Nipissing ecoregion between Blind River and Sudbury, Ontario. The first gypsy moth outbreaks in the region occurred between 1993 and 1996 (Evans et al. 1997; Nealis et al. 1999), and a less severe outbreak took place from 2001 to 2003 (Hopkin and Scarr 2003). All ten locations were xeric, rocky, upland sites, and stand composition at each was at least 50% red oak.

Biweekly collections of caterpillars were made from burlap bands on 50 hardwood trees at each of the ten sites from May through August in 2006 and 2007. Sample trees at each site included 30 red oak and 10 each of the second and third most abundant tree species at the site: either trembling, *Populus*

tremuloides Michaux, or large-tooth, *P. grandidentata* Michaux, aspen; red, *Acer rubrum* L., or sugar *A. saccharum* Marsh, maple; white birch *Betula papyrifera* Marsh; or black ash *Fraxinus americana* L. Burlap bands were placed at approximately 1.3 m above the ground; caterpillars were collected from on top of, underneath and nearby the bands during each visit. Caterpillars were placed in individual, clear plastic cups with lids and reared on fresh host tree leaves. Caterpillars were monitored and fed daily from collection until pupation or death. Dead caterpillars were observed for up to a week afterwards to check for parasitoid emergence. Lepidopteran and emerged parasitoid pupae were checked daily until adult emergence. Species requiring a period of overwintering before emergence were placed in vermiculite and kept outside over the winter. Adult moths and parasitoids were preserved, pinned and labeled.

Identification of caterpillars occurred as soon as possible after collection using a variety of field guides and online resources (Troubridge and Lafontaine 2004; Wagner 2005; Opler et al. 2009). Adult moths were used to confirm or correct larval identifications. When identification was not possible, for example because of failed adult emergence, caterpillars were left with a morphospecies designation. Adult hymenopterans were identified using keys to the parasitoids of well-known pest species (Simons et al. 1979; Williams et al. 1996) as well as keys to the families and genera of parasitic Hymenoptera (Goulet and Huber 1993; Gibson et al. 1997). Tachinid flies are notoriously difficult to rear in the laboratory (e.g. Sipell 1961; Williams et al. 1996), and many in this study did not emerge as adults. For this reason, we assigned all tachinid puparia to a morphospecies and, when possible, used keys to puparia to identify them to species (Sipell 1961; Simons et al. 1979). We also compared the morphospecies with puparia and adult tachinids in the Canadian National Collection (CNC) of insects in Ottawa, Ontario, and thus assigned tentative species names to the specimens. Expert taxonomists at the CNC confirmed, corrected, and carried out identifications of both hymenopteran (A. Bennett, J. Fernandez Triana, G. Gibson, H. Goulet, J. Huber) and dipteran (J. O'Hara) parasitoids. Voucher specimens have been placed in the Forest Entomology lab at the University of Toronto (Lepidoptera, Diptera) as

well as in the CNC (Hymenoptera). Host-parasitoid associations were checked using Arnaud (1978) for the Diptera and the program Taxapad (Yu 2009) for the Hymenoptera.

Estimated parasitoid sharing

For each parasitoid species, we calculated the average number of individuals that emerged from gypsy moth per site per year. We did the same for parasitoids that emerged from all native caterpillars. All averages were square-root transformed to clarify graphical display, but quantitative conclusions were not altered by the transformations. We calculated 95% confidence intervals for the averages using the percentile bootstrap method (Efron and Tibshirani 1993), resampling sites—but not years—with replacement; this resampling plan is appropriate because years were not randomly sampled. We then plotted the estimates for each parasitoid species on a scatterplot with natives on the y-axis and gypsy moth on the x-axis. Axes were on the square-root scale so that the units of the axes could be reported as number of parasitized individuals per site per year. If all parasitoids are specialists on either gypsy moths or natives, then all points should lay along the x-axis or y-axis, respectively. Shared parasitoids lie off of the axes (Fig. 1a). For clarity, confidence intervals were only displayed for parasitoids with some degree of sharing.

Quantitative food web construction

Quantitative food webs were constructed using the graphics package within the R system for statistical computing (R Development Core Team 2007). Bars at the bottom of each graph represent hosts (caterpillars) and bars at the top represent parasitoids. The width of each bar is proportional to the relative abundance of that species in the total number of hosts or parasitoids, respectively. Only parasitized hosts were included in the quantitative food webs; therefore the relative host abundances shown are not representative of the entire community of collected caterpillars. However, as the collected caterpillar species that did not produce parasitoids made up less than three percent of the total number of individuals collected, their absence from the food webs does not cause a noticeable difference in the calculated total

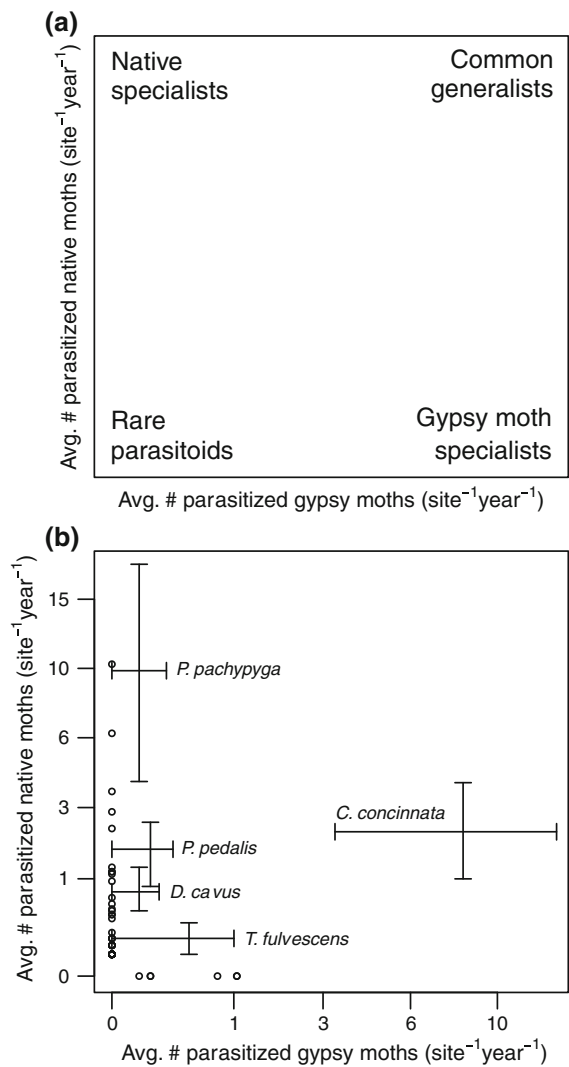


Fig. 1 Estimates of parasitoid sharing between gypsy moth and native species. Parasitoid species are plotted along two square root-scaled axes: average number of parasitized native moths (y-axis) versus gypsy moths (x-axis). Panel (a) illustrates how to interpret the data in panel (b) by classifying parasitoids into four categories: native specialists, gypsy moth specialists, rare parasitoids, and common generalists. Percentile bootstrap 95% confidence intervals are shown as error bars for the only five species for which some degree of sharing was observed: *C. concinnata*, *P. pachygyga*, *P. pedalis*, *D. cavus* and *T. fulvescens*

host abundances. The width of each wedge connecting hosts and parasitoids is proportional to the relative abundance of that particular host-parasitoid interaction within all host-parasitoid interactions observed for that parasitoid. The order of hosts and

parasitoids within each food web was determined using an algorithm to minimize overlap provided by the `plotweb` function in the `Bipartite` package for R (Dormann et al. 2009). Quantitative food webs were constructed for pooled host-parasitoid interactions summarizing each site type in both sampling years as well as for each individual site in both sampling years.

Quantitative food web metrics

We calculated quantitative versions of four common food web metrics for both summary and individual webs, including: connectance (C); linkage density (LD); generality (G); and, vulnerability (V). We define connectance as the ratio of the number of realized links (L) in the web divided by the total number of possible links. We follow the recommendations of Valladeres et al. (2001) for host-parasitoid food webs and calculate the total number of possible links as the number of hosts (H_p) multiplied by the number of parasitoids (P) rather than as a factorial of the total number of species in the web ($N(N - 1)$); the latter allows for unrealistic within-trophic level feeding interactions while the former does not. Linkage density is the number of realized links divided by the number of species in the web, $L/(H_p + P)$. Generality is a measure of the number of hosts per parasitoid (H_p/P) and vulnerability is a measure of number of parasitoids per host (P/H_p).

Quantitative versions of the above metrics (C_q , LD_q , G_q , V_q) as well as interaction evenness (IE) and compartment diversity were calculated following Bersier et al. (2002) and Tylianakis et al. (2007). These quantitative metrics are based on Shannon's diversity index, H, and account for the magnitude of each interaction within the web in addition to its presence or absence. Interaction evenness is similar to community evenness, and describes the dominance of particular host-parasitoid interactions within the web; a value of 1.00 would imply that all interactions are equally represented while lower values indicate that some interactions are more dominant than others. A compartment is defined as a sub-web within the web that is not connected to any other sub-web, and compartment diversity is a measure of the abundance and richness of host and parasitoid species within the compartment.

Statistical tests

All tests were performed in R (R Development Core Team 2007), with the use of the packages `nlme` (Pinheiro et al. 2007) and `vegan` (Oksanen et al. 2006). To assess whether gypsy moth outbreak history (yes or no) or current abundance had any effect on quantitative food web structure it was of interest to us to test the response of the calculated quantitative metrics to the predictor variables; however, the number of individual metrics would mean a large number of tests and an increased chance of committing a type I error. To avoid this problem, we used analysis of dissimilarities (ADONIS) (with Bray-Curtis distances) to test the effects of the predictor variables on the entire group of quantitative food web metrics as a multivariate response matrix (McArdle and Anderson 2001). In addition to this method, we also performed mixed effects modeling as described above to test individual metric responses to sample year (2006 or 2007) and either gypsy moth history (yes or no) or \log_{10} (gypsy moth abundance), in case the multivariate tests masked significant individual responses. We addressed the issue of multiple comparisons in these tests by using the Benjamini and Hochberg (1995) correction for *P*-values to control for false discovery rates.

We tested the effects of gypsy moth on the richness of parasitoids of different types and trophic levels. Thus, we used two sets of mixed effects models to test the effects of sample year (2006 or 2007) and either gypsy moth history (yes or no) or \log_{10} (gypsy moth abundance) on the richness of: (1) non-gypsy moth primary parasitoids; (2) secondary parasitoids; and, (3) total parasitoids. Mixed effects models were chosen because, by modeling site identification as a random effect, they can account for the fact that the data include two observations from each of the ten sites (Lindstrom and Bates 1990; Zuur et al. 2009). Model-fitting and checking procedures were carried out as recommended in Zuur et al. (2009).

Finally, because we found that *Compsilura concinnata* (Meigen) was the only generalist that attacked both gypsy moth and native caterpillars in substantial numbers, we used a variety of methods to explore potential effects of gypsy moth on the community of caterpillars attacked by *C. concinnata*. We performed mixed effects modeling as described

above, testing the effects of sample year and either gypsy moth history or $\log_{10}(\text{gypsy moth abundance})$ on *C. concinnata* host richness. We also asked if *C. concinnata* switch to gypsy moth at high gypsy moth abundances; such switching would suggest that the effect of *C. concinnata* on native caterpillars is buffered by the gypsy moth, while the gypsy moth is present. To assess this idea we conducted a binomial generalized linear model (glm) to test if the number of *C. concinnata* reared from gypsy moth versus non-gypsy moth hosts was related to sample year and gypsy moth abundance. To conduct a valid test, we need to account for the fact that the number of *C. concinnata* reared from gypsy moth is necessarily correlated to gypsy moth abundance; to do this, we compared the observed logit-scale slope with a distribution of slopes under the null hypothesis that the expected proportion of gypsy moth that are attacked by *C. concinnata* is constant at all levels of gypsy moth abundance. This null distribution was approximated by 10,000 randomizations of the *C. concinnata*-host relationships, keeping the total numbers of the parasitoid, gypsy moth and non-gypsy moth hosts observed fixed at each site combination.

Results

Parasitism rates and parasitoid sharing

We reared 71 species of parasitoid from over 1,250 parasitized host caterpillars representing 37 lepidopteran species (Tables S1–S3 in Online Resource 1). A small percentage of the parasitoid species we reared were non-native; these include two flies and three wasps that were introduced as biological control agents for the gypsy moth as well as one accidentally introduced eulophid wasp. Only one of the host species in the food webs, the gypsy moth, was non-native. We reared eight primary and two secondary parasitoids from the gypsy moth; in addition to the six introduced biological control agents we found two native primary and two native secondary parasitoids. In general gypsy moth parasitism rates were very low—out of 3,849 gypsy moth caterpillars collected only 233 were parasitized. Parasitism rates ranged from zero to 24%, with an average of $3.04 \pm 1.05\%$ in 2006 and $7.17 \pm 2.23\%$ in 2007. By far the most abundant gypsy moth parasitoid was the introduced

tachinid *C. concinnata*, which parasitized an average of $2.54 \pm 1.02\%$ and $5.87 \pm 2.27\%$ of the gypsy moth in 2006 and 2007, respectively. We reared *C. concinnata* from eight identified host species, five of which were known hosts and three of which represent new rearing records (Table S3 in Online Resource 1). Of the remaining total 105 lepidopteran species collected in our study, 11 are known to be hosts of the introduced tachinid (Raizenne 1952; Arnaud 1978; Peigler 1994; Cossentine and Jensen 1995; Strazanac et al. 2001) but did not produce any adult *C. concinnata* in our rearings.

Gypsy moth shared few parasitoids with native hosts (Fig. 1b). Only five of the 71 collected parasitoids were reared out of both gypsy moth and at least one other species. Only one of those five species, *C. concinnata*, was reared out of more than one gypsy moth per site per year on average. Therefore, in our study system, any potential parasitoid-mediated indirect effects of gypsy moth on native caterpillars (e.g. apparent competition) will likely involve *C. concinnata*.

Gypsy moth and food web structure

The summary quantitative food webs for sites with no gypsy moth history in 2006 is dominated by white-marked tussock moth, *Orgyia leucostigma* (J.E. Smith), and forest tent caterpillar, *Malacosoma disstria* Hübner, parasitoids (Fig. 2a); in addition, this web has more species and links and greater interaction evenness than the other three (Table 1). The other three webs are similar to each other and are dominated by forest tent caterpillar parasitoids, despite the fact that gypsy moth is the numerically dominant host in each one (Fig. 2b–d). All four of the food webs contain many single host-parasitoid compartments as well as one larger multi-species compartment; less common caterpillars are connected with more dominant species by means of generalist parasitoids in the large compartment. This can also be seen in the individual site food webs, represented by the sites Agnew East (no GM history) and Wavy (GM history) (Fig. S1 in Online Resource 1) from 2006. Means and standard errors for quantitative food web metrics for individual sites over both years are summarized in Table 2.

None of the predictor variables had significant relationships with the suite of quantitative food web

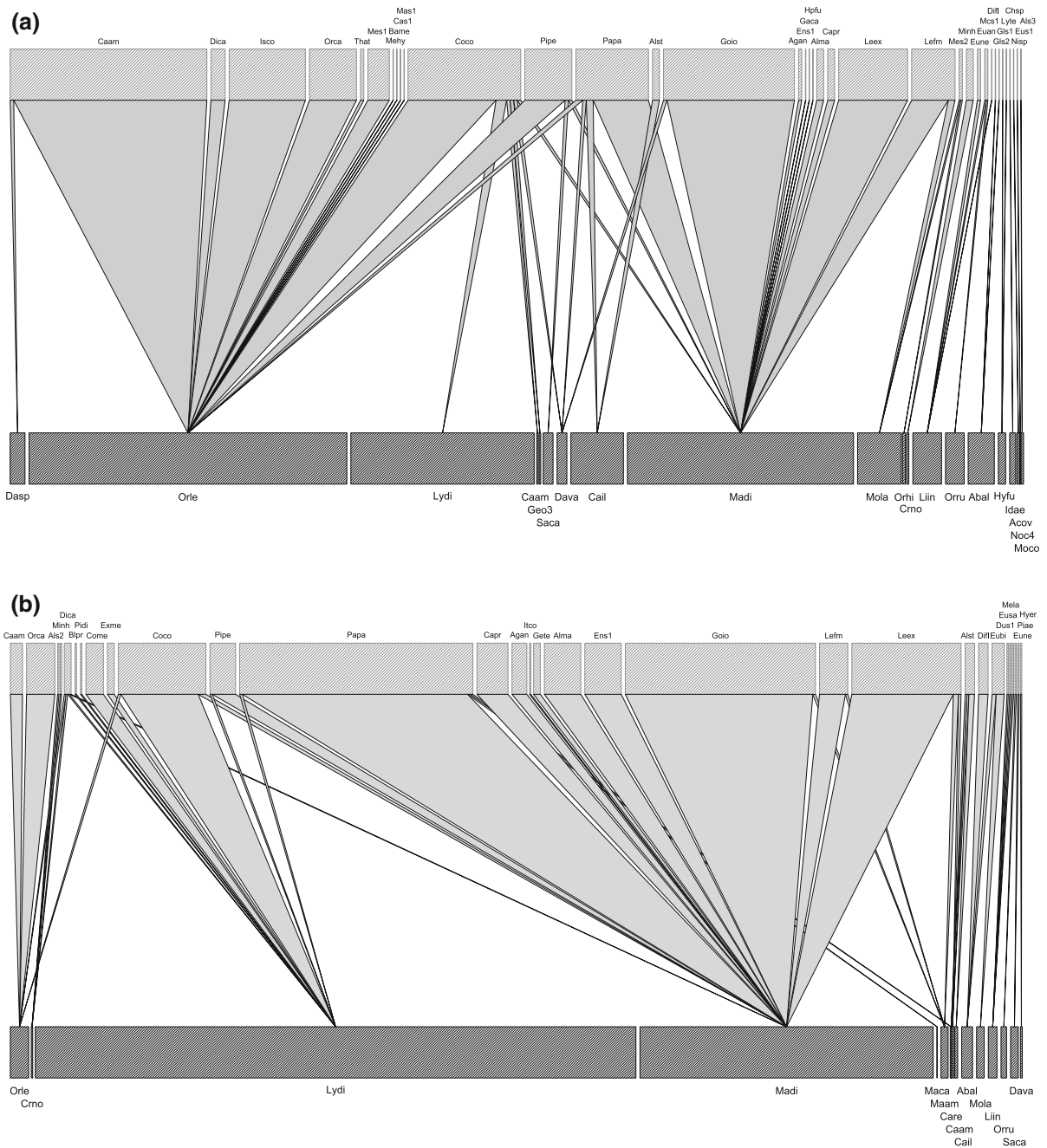


Fig. 2 Summary quantitative food webs for: **a** sites with no history of gypsy moth outbreak in 2006; **b** sites with histories of gypsy moth outbreak in 2006; **c** sites with no history of gypsy moth outbreak in 2007; and, **d** sites with histories of gypsy moth outbreak in 2007. Lower bars represent hosts (caterpillars) and upper bars represent parasitoids; the width of each bar is proportional to the relative abundance of that species among all

parasitized hosts or all parasitoids, respectively. The width of the wedge linking host and parasitoid is proportional to the relative abundance of that host within all hosts from which that parasitoid was reared; for example, parasitoid Caam was reared once from host Dasp and 58 times from host Orle. Species codes are given in Electronic Supplementary Material Table S1 for hosts and Table S2 for parasitoids

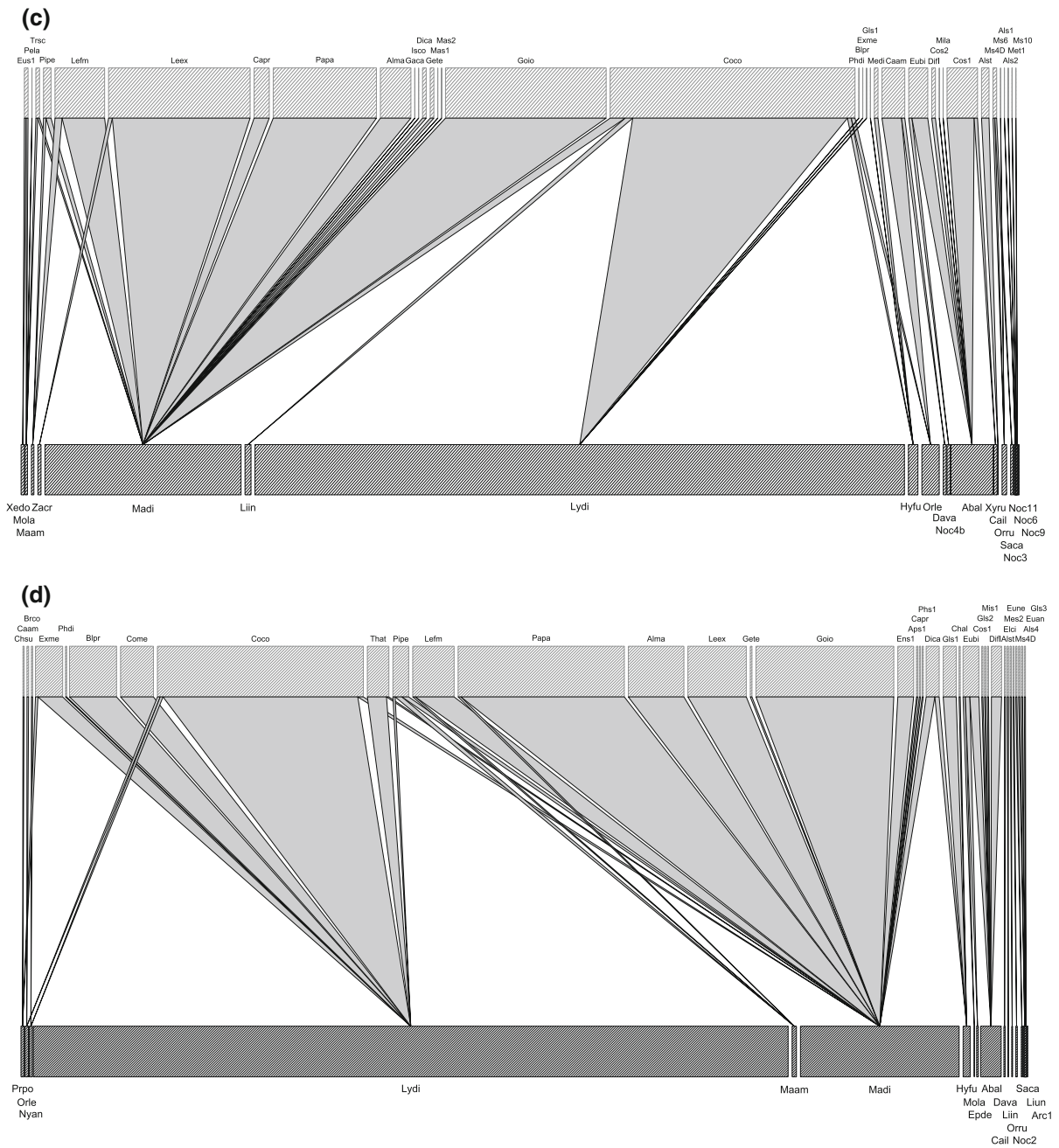


Fig. 2 continued

metrics analyzed as a multivariate response matrix (Tables 3, 4). Univariate mixed effects models also showed no effects of gypsy moth history and sample year on individual quantitative food web metrics, although generality was marginally significantly ($t_9 = -2.23$, $P = 0.05$) higher in 2006 than in 2007. However, after adjusting the P -values to correct for

multiple comparisons this effect was no longer significant (Table 3). Similarly, univariate mixed effects models showed no effects of gypsy moth abundance and sample year on individual food web metrics, either before or after P -value adjustments (Table 4). We found no detectable effects of gypsy moth on native food web structure.

Table 1 Descriptive statistics for summary quantitative food webs of caterpillars and their parasitoids collected at sites with ($n = 5$) and without ($n = 5$) histories of significant gypsy moth defoliation in both 2006 and 2007

Food web descriptor	2006		2007	
	No history	GM history	No history	GM history
Collected host species abundance	863	1,973	1,443	2,204
Collected host species richness (Hc)	58	46	38	41
Parasitized host species richness (Hp)	20	15	20	18
Parasitoid richness (P)	36	30	35	36
Number of associations (L)	51	46	48	48
Quantitative generality	1.36	1.24	1.29	1.19
Quantitative vulnerability	5.77	5.90	4.75	5.08
Quantitative connectance	0.06	0.08	0.05	0.06
Quantitative linkage density	3.56	3.57	3.02	3.14
Quantitative interaction evenness	0.53	0.46	0.49	0.48
Number of compartments	9	6	8	10
Diversity of compartments	4.13	3.01	3.98	4.88

Table 2 Mean (± 1 SE) descriptive statistics for individual quantitative food webs of caterpillars and their parasitoids collected at sites with ($n = 5$) and without ($n = 5$) histories of significant gypsy moth defoliation in both 2006 and 2007

Food web descriptor	2006		2007	
	No history	GM history	No history	GM history
Collected host species abundance	176.6 \pm 11.9	399.2 \pm 141.3	288.8 \pm 42.1	441.4 \pm 95.3
Collected host species richness (Hc)	23.6 \pm 1.5	20.0 \pm 1.0	17.6 \pm 1.3	17.6 \pm 1.6
Parasitized host species richness (Hp)	7.4 \pm 0.9	7.0 \pm 1.1	7.6 \pm 1.4	6.6 \pm 1.3
Parasitoid richness (P)	15.0 \pm 1.6	14.2 \pm 2.1	14.8 \pm 2.0	14.6 \pm 1.9
Number of associations (L)	18.2 \pm 2.0	16.4 \pm 2.9	17.0 \pm 2.8	16.4 \pm 2.4
Quantitative generality	1.27 \pm 0.09	1.16 \pm 0.09	1.16 \pm 0.05	1.12 \pm 0.05
Quantitative vulnerability	4.39 \pm 0.49	4.00 \pm 0.96	3.67 \pm 0.65	3.33 \pm 0.60
Quantitative connectance	0.13 \pm 0.01	0.13 \pm 0.02	0.11 \pm 0.01	0.11 \pm 0.02
Quantitative linkage density	2.83 \pm 0.23	2.58 \pm 0.46	2.41 \pm 0.32	2.23 \pm 0.29
Quantitative interaction evenness	0.62 \pm 0.03	0.57 \pm 0.07	0.59 \pm 0.07	0.56 \pm 0.08
Number of compartments	4.40 \pm 0.93	5.00 \pm 0.32	5.40 \pm 0.51	4.80 \pm 1.36
Diversity of compartments	3.77 \pm 0.57	3.62 \pm 0.48	4.13 \pm 0.30	4.02 \pm 1.45

Gypsy moth and parasitoid diversity

Neither gypsy moth history nor abundance were significantly related to the richness of any of the tested parasitoid groups or trophic levels (Tables 5, 6). We did not detect a relationship between gypsy moth abundance and: (1) the richness of non-gypsy moth primary parasitoids; (2) secondary parasitoids; or, (3) total parasitoid richness.

C. concinnata and gypsy moth

The richness of host species attacked by *C. concinnata* was not significantly related to gypsy moth history ($t_8 = -1.20$, $P = 0.26$) or sample year ($t_9 = 0.71$, $P = 0.50$) in a mixed effects model with both predictor variables. Neither was it related to \log_{10} (gypsy moth abundance) ($t_8 = -0.79$, $P = 0.45$) or sample year ($t_8 = 1.04$, $P = 0.33$) in a second mixed effects

Table 3 The effects of gypsy moth outbreak history and sample year on quantitative food web metrics, tested as a multivariate response matrix using analysis of dissimilarities (ADONIS) and as individual response variables using mixed effects models; adjusted *P*-values were obtained using the Benjamini-Hochberg correction for multiple comparisons

Response variable	Multivariate ADONIS			
	Predictor	F	R ²	<i>P</i>
All quantitative food web metrics	Year	0.49	0.03	0.61
	GM history	0.16	0.01	0.83
Response variable	Univariate mixed effects models			
	Predictor	t _g	<i>P</i>	<i>P</i> _{adj}
Generality	GM history	-0.75	0.47	1.00
	Year	-2.23	0.05	0.35
Vulnerability	GM history	-0.44	0.67	1.00
	Year	-1.38	0.20	0.47
Linkage density	GM history	-0.55	0.60	1.00
	Year	-1.52	0.16	0.47
Connectance	GM history	0.00	1.00	1.00
	Year	-1.14	0.29	0.51
Interaction evenness	GM history	-0.59	0.57	1.00
	Year	-0.40	0.70	0.70
Number of compartments	GM history	0.00	1.00	1.00
	Year	0.48	0.65	0.70
Compartment diversity	GM history	0.16	0.88	1.00
	Year	0.93	0.38	0.53

Table 4 The effects of log₁₀(gypsy moth abundance) and sample year on quantitative food web metrics, tested as a multivariate response matrix using analysis of dissimilarities (ADONIS) and as individual response variables using mixed effects models; adjusted *P*-values were obtained using the Benjamini-Hochberg correction for multiple comparisons

Response variable	Multivariate ADONIS			
	Predictor	F	R ²	<i>P</i>
All quantitative food web metrics	Year	0.52	0.03	0.57
	GM abundance	1.28	0.07	0.31
Response variable	Univariate mixed effects models			
	Predictor	t _g	<i>P</i>	<i>P</i> _{adj}
Generality	GM abundance	-1.29	0.23	0.42
	Year	-0.16	0.88	0.88
Vulnerability	GM abundance	1.22	0.26	0.42
	Year	-1.85	0.10	0.35
Linkage density	GM abundance	1.11	0.30	0.42
	Year	-1.87	0.10	0.35
Connectance	GM abundance	0.80	0.45	0.45
	Year	-1.37	0.21	0.37
Interaction evenness	GM abundance	-1.61	0.15	0.42
	Year	0.53	0.61	0.72
Number of compartments	GM abundance	-0.87	0.41	0.45
	Year	0.87	0.41	0.57
Compartment diversity	GM abundance	-1.21	0.26	0.42
	Year	1.45	0.19	0.37

model. The number of *C. concinnata* reared from gypsy moth versus non-gypsy moth hosts increased significantly with gypsy moth abundance (randomization test: slope = 2.45, *P* < 0.001) (Fig. 3), but was not significantly related to sample year (slope = 3.20, *P* = 0.39).

Discussion

We found minimal impact of the gypsy moth on native host-parasitoid food webs in northern temperate forests, where gypsy moth is a recent introduction. Neither gypsy moth outbreak history nor current abundance had any significant effects on the richness of non-gypsy moth parasitoids or on the structure of quantitative food webs, even when gypsy moth was the most abundant host species in the web. Parasitism of the gypsy moth was low, and involved mostly introduced parasitoids

that were not found attacking native caterpillars; therefore, we should not expect gypsy moth to have strong parasitoid-mediated effects on native food webs. Furthermore, the only gypsy moth parasitoid that was found attacking native species in significant numbers, *C. concinnata*, increased its specialization on gypsy moth at high gypsy moth abundances, paradoxically reducing the impact of the invasive herbivore on native food webs at high population levels, while gypsy moth was present. Here we discuss some key findings of the study, as well as the resulting implications for invasion biology and the management of invasive forest insect pests.

Limited impact of the gypsy moth

Neither the richness of other primary parasitoids nor that of secondary parasitoids was significantly affected by gypsy moth abundance or outbreak

Table 5 Mixed effects models testing the effects of gypsy moth outbreak history and sample year on measures of parasitoid richness, reared from caterpillars collected using

burlap bands at sites with (n = 5) and without (n = 5) gypsy moth outbreak history in 2006 and 2007

Response variable	Coefficient	Estimate	SE	df	t	Pr(>t)
Richness of non-GM 1° parasitoids	GM history	-1.50	1.10	8	-1.37	0.21
	Sample year	-0.30	1.05	9	-0.28	0.78
Richness of 2° parasitoids	GM history	-0.50	0.89	8	-0.56	0.59
	Sample year	0.30	0.79	9	0.38	0.71
Total parasitoid richness	GM history	-0.60	2.14	8	-0.28	0.79
	Sample year	0.20	1.48	9	0.13	0.90

Table 6 Mixed effects models testing the effects of \log_{10} (gypsy moth abundance) and sample year on measures of parasitoid richness, reared from caterpillars collected

using burlap bands at sites with (n = 5) and without (n = 5) gypsy moth outbreak history in 2006 and 2007

Response variable	Coefficient	Estimate	SE	df	t	Pr(>t)
Richness of non-GM 1° parasitoids	GM abundance	-0.44	0.86	8	-0.52	0.62
	Sample year	0.09	1.32	8	0.07	0.95
Richness of 2° parasitoids	GM abundance	-0.02	0.67	8	-0.03	0.98
	Sample year	0.32	0.99	8	0.32	0.76
Total parasitoid richness	GM abundance	1.65	1.47	8	1.13	0.29
	Sample year	-1.26	1.95	8	-0.65	0.54

history, indicating that the presence of gypsy moth has little indirect effect on native parasitoid richness. This is in contrast with the results of Eveleigh et al. (2007), who found that increases in spruce budworm, *Choristoneura fumiferana* (Clemens), densities were related to decreases in non-budworm primary parasitoids and increases in hyperparasitoids. They describe this as a birdfeeder effect, whereby primary parasitoids respond to increases in budworm density by switching to attacking it instead of less abundant host species, followed by an increase in hyperparasitoids in response to the primary parasitoids. Although not an invasive species, the spruce budworm is similar to the gypsy moth in that it is a spring-feeding herbivore with periodically extremely abundant populations; one might expect the parasitoid communities to respond in the same way. However, as our study has shown, there has been very little recruitment of native primary parasitoid species to the gypsy moth or of native hyperparasitoids to introduced gypsy moth parasitoids—processes that would be necessary in order for the birdfeeder effect to occur. Thus, the opportunities for gypsy moth to indirectly affect native species via shared natural

enemies seem to be very limited, at least in these study sites. There is some evidence that this result might also hold true in areas where gypsy moth has been established for longer; in a study of the parasite complexes of both gypsy moth and forest tent caterpillar in New York, Eggen (1988) found that neither caterpillar had significant influences on the parasite complex of the other. It is of interest to note that Eggen (1988) detected no parasitoid-mediated interactions between gypsy moth and forest tent caterpillar despite finding higher levels of parasitism (up to 38%) than observed in our study.

The limited opportunity for interaction within the food webs is reflected in the finding that neither gypsy moth history nor current abundance had significant effects on the vulnerability, connectance, linkage density, or interaction evenness in quantitative food webs. These minimal effects are consistent with the low level of shared parasitism that we observed between the gypsy moth and native species. It is difficult to compare these results with others as no other study has used quantitative food webs to investigate the impacts of an invasive herbivore. Recent applications of quantitative food webs have all

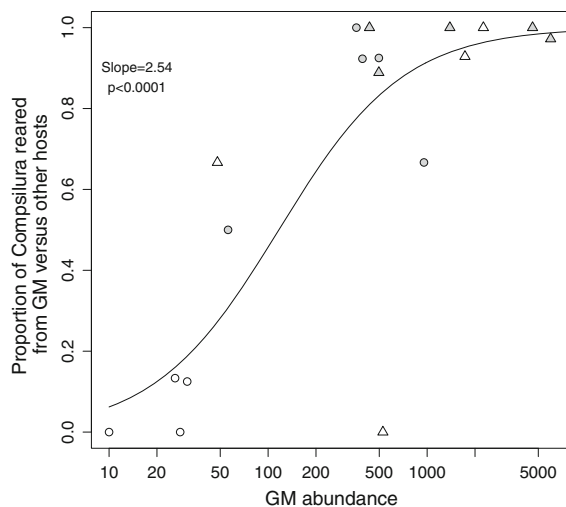


Fig. 3 Proportion of the introduced tachinid parasitoid *Compsilura concinnata* (Meigen) reared from gypsy moths relative to other hosts in relation to total observed gypsy moth abundance at sites with (triangles) and without (circles) histories of gypsy moth outbreak in 2006 (open shapes) and 2007 (grey-filled shapes)

been based on the hypothesis that bottom-up differences in vegetation and habitat will cause effects at higher trophic levels (Tylianakis et al. 2007; Heleno et al. 2008; Henson et al. 2009), whereas our study explored the effects caused by the addition of a species at the middle trophic level. Morris et al. (2004) tested the effects of herbivore removal on quantitative food webs, and found reduced parasitism and higher densities of herbivores that shared parasitoids with the removed species. However, they specifically chose their focal species for removal based on the connections within the web that showed the most potential for indirect interactions. Our study involved the ‘natural experiment’ of species invasion, and found little potential for indirect interaction within the food webs. Furthermore, all of the food webs in this study exhibited low levels of connectance and a relatively high number of compartments—on average about two compartments less than the number of species in the web. The lack of connectance illustrates the low level of shared parasitism between all species that we observed, not just between the gypsy moth and native species. The connections between compartments that did exist were caused in the large part by relatively rare interactions between forest tent caterpillar parasitoids and other species, as well as by the generalist *C. concinnata*.

Compsilura concinnata was the most generalist species in this study, as well as the only introduced parasitoid that was reared from native species in significant numbers. Although *C. concinnata* is known as an extreme generalist, the results of this study indicate that it does have some degree of preference—the only species that we reared it from more than once or twice were the gypsy moth, whitemarked tussock moth, and forest tent caterpillar. Tachinids in general exhibit preferences for hairy, large, and gregarious caterpillars (Weseloh 1980; Stireman and Singer 2003), characteristics possessed by those three caterpillar species. Furthermore, we found that *C. concinnata* became more of a specialist when gypsy moth was the most abundant species across all sites. Specifically, the proportion of *C. concinnata* reared from gypsy moth versus non-gypsy moth hosts increased significantly with gypsy moth abundance. Similarly, Eggen (1988) found evidence that *C. concinnata* preferred forest tent caterpillar to gypsy moth when it was the more abundant species.

This host-switching response is known from other generalist parasitoids (Cornell and Pimentel 1978) and has been suggested as a mechanism for promoting coexistence and stability in community dynamics (Abrams and Matsuda 1996; Hassell 2000). It may indeed have acted in this fashion in this study; *C. concinnata* was the only parasitoid in the food webs with any potential to cause negative indirect effects, however it was reared less often from native species at sites with high gypsy moth populations. The parasitoid’s multivoltine life history complicates this interpretation somewhat, as second generation progeny produced from gypsy moths must have used some native species as hosts; however, *C. concinnata* was reared from very few late season species collected in this study. Targeted studies of late season species known to be attacked by *C. concinnata* would be useful to address this issue.

Alternative explanations

We interpret our results as evidence of a limited impact of the gypsy moth on native food webs, as this interpretation is the most parsimonious given the available data; however, other alternatives exist. As with all studies of mobile animal communities, it is possible that our burlap band collection method biases our inferences of the native food web. In

particular, the use of burlap bands as a collection method can increase estimates of parasitism rates in at least two species of tachinids (Reardon 1976; Gould et al. 1992). However, given that our results include very low levels of observed gypsy moth parasitism, the fact that our collection technique may have artificially increased gypsy moth parasitism rates would not affect the direction of our conclusions and in fact would cause them to be more conservative. In addition, burlap bands are best at capturing species such as the gypsy moth that rest on the trunks of trees during the day and are known to be more effective for certain families of Lepidoptera than for others (Butler and Strazanac 2000); thus, we did not thoroughly sample all species of native caterpillar present in these forests.

We chose the burlap band collection method despite its limitations for several reasons: we were interested in sampling caterpillars that were most likely to share parasitoids with the gypsy moth, and parasitoids are known to attack species within similar habitats and with similar ecological characteristics (e.g. Stireman and Singer 2003). In addition, the use of burlap bands has been demonstrated to be effective at sampling gypsy moths as well as other groups of caterpillars (Raimondo et al. 2004) and is an inexpensive, efficient, and easily replicated technique. However, we acknowledge that this method will not have captured all potential hosts of the parasitoids that were reared and thus the food webs do not reflect the entire set of host-parasitoid interactions that exist in these communities. For example, we collected very few saturniid species; a group whose population declines in the northeastern United States have been attributed to *C. concinnata* (Boettner et al. 2000; Kellogg et al. 2003). It is unknown if saturniid populations in our study region have declined or not; there are already fewer species of saturniids in northern temperate forests than in more southern areas (Riotte 1992; Tuskes et al. 1996). However, we can anecdotally report that numerous adults of a variety of saturniid species (*Dryocampa rubicunda* [Fabricius], *Eacles imperialis* [Drury], *Hyalophora cecropia* [Linnaeus], *Actias luna* L., and *Antheraea polyphemus* [Cramer]) were observed at campground blacklights near Espanola, ON, during the summers of 2006 and 2007 (L. Timms, personal observation).

In addition to the possibility that we did not observe any effects of the gypsy moth because the

collection technique was not suitable for susceptible species, it is possible that these vulnerable species may have dropped out of the food webs immediately after gypsy moth invasion in the region and that this study took place too late to capture their decline. This may be the case with saturniids, as other studies using burlap have collected at least one species, *Hemileuca maia* (Drury) (Lepidoptera: Saturniidae), in greater numbers than we did (Wagner et al. 1995; Butler and Strazanac 2000). These issues could be addressed by deploying sentinel populations of potentially vulnerable species in our sites and monitoring their survival and parasitism rates, as has been done in Massachusetts (Boettner et al. 2000; Selfridge et al. 2007) and Virginia (Kellogg et al. 2003).

Another possibility is that our study took place too early to capture any effects of gypsy moth; the concept of extinction debt suggests that there can be a significant time lag before the effects of invasive species can be detected in changes to the native community (Kuussaari et al. 2009). In this case it would be informative to return to these sites in the future and evaluate any long-term impacts the gypsy moth may have had on the native host-parasitoid food webs. It may also be possible to compare food webs along a historical gradient of gypsy moth establishment, but a lack of baseline data and sites with different bio-geographical characteristics makes these comparisons difficult. A major contribution of our study is thus that it could act as a baseline for future work.

Conclusions

We found minimal impacts of an invasive herbivore on native herbivore-parasitoid food webs. Previous work with these data has shown that gypsy moth does have some impact on the richness and structure of late-season feeding caterpillar communities (Timms 2010). However, this impact was due to current gypsy moth abundance and not outbreak history, suggesting that it is the role of gypsy moth as an outbreak species that mediates its impact instead of the fact that it is an invasive species. Our findings using quantitative food webs are consistent with this conclusion; moreover, as gypsy moth has little effect on the native parasitoid community, its impacts on native caterpillars are likely due to feeding-induced changes in host tree

foliage. These changes are more likely to be effected at high gypsy moth populations, and also to affect species that feed later in the year once the gypsy moth has completed its development.

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